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# THE HEAD STRUCTURES OF THE ORTHOPTERON STENOPELMATUS—A CONTRIBUTION TO THE STUDY OF THE EXTERNAL ANATOMY OF STENOPELMATUS

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The main features of the head, thorax and abdomen of the "sand cricket" *Stenopelmatus* will be discussed in three papers dealing with the external anatomy of this extremely interesting, primitive and common insect, which is exceptionally suitable for anatomical study. The specimens used in this study were given to me by Dr. S. B. Freeborn, to whom I am deeply indebted for much valuable material.

Viewed from the front, the head capsule of *Stenopelmatus* (Fig. 5) is somewhat oval in outline, and is markedly rounded above. Its surface is quite hard and smooth, due, doubtless, to the fact that the insect uses its head and stout mandibles in digging. The huge muscle bundles inserted upon the inner surface of the skull show through the rather transparent head capsule in specimens preserved in alcohol and appear to divide the surface of the head into symmetrically arranged areas, but these have no especial value for the study of comparative morphology. The coronal suture *cs* of Fig. 5 (representing the stem of the Y-shaped epicranial suture) is rather faint, and the frontal sutures *fs* (representing the arms of the Y-shaped epicranial suture) are very indistinct; they extend just back of and above the raised area or frontal prominence above the letter *f* in Fig. 5.

The regions on each side of the coronal suture *cs* are the parietals *pa* (Fig. 5). The temples *te* or areas above and behind the eyes *e* are called the tempora. The cheeks, or regions below and behind the eyes *e* are called the genæ, *ge*. Below each gena *ge* is a sclerite *bm* variously termed the basimandibulare, mandibulare, and trochantin of the mandible. It is demarked posteriorly by the basimandibular suture *es* which extends mesad toward its fellow on the opposite side of the head, but the two sutures do not meet in *Stenopelmatus,* as they do in some Orthoptera in which the complete suture extending across from one side to the other is called the epistomal suture. In such cases that portion of the epistomal suture between the frons *f* and the posterior clypeal region *pc* is called the frontoclypeal suture, while the lateral portions of the epistomal suture form the basimandibular sutures. In *Stenopelmatus,* the sutures, labeled *es* in Fig. 5, mark the location of the invaginations forming the anterior arms of the tentorium, labeled *pt* in Fig. 6, and since the sutures *es* correspond to the frontal pits of other insects (in which the frontal pits mark the location of the invaginations forming the anterior arms of the tentorium) they are also labeled *fp* to denote this fact. The frons, or front, labeled *f* in Fig. 5, is the area between the frontal sutures *fs* and the frontal pits *fp*. As was mentioned above, the frons is sometimes separated from the clypeus by a frontoclypeal suture (also called the clypeal suture). The clypeus is composed of two areas, the postclypeus, or epistoma *pc,* and the anteclypeus *ac*. The postclypeus *pc* is usually more darkly pigmented, and the anteclypeus *ac* is usually pale, resembling membrane in color. The suture between the clypeus and the labrum *l* is called the clypeolabral suture, or simply the labral suture. On the oral or pharyngeal surface (i. e., roof of the mouth cavity) the boundary between the labium and clypeus is marked by the tormæ described later.

The term "epicranium" is used very loosely even by recent entomologists. Thus Imms (1925) does not include the frons in the epicranial area, while Comstock (1924) states that "Under the term 'epicranium' are included all of the paired sclerites of the skull and sometimes also the front." Snodgrass (1928) includes not only the frons but also the clypeus, etc., in the designation epicranium, and there seems to be no uniformity in the application of the term. If it be employed at all, it is preferable to restrict the designation epicranium to the paired sclerites and frons, but not including the clypeus, etc. The designation vertex is also employed in various ways by different entomologists, but it is preferable to restrict its application to the upper portion of the head capsule, a vague area on the top of the head, but not extending down the front of the face, as Yuasa (1920) and others maintain.

The faintly demarked ring about the base of the antenna (*an* of Figs. 5 and 11) is called the antennale. It bears an antennifer, *af* of Fig. 11, or projection near the base of the antenna, which is fairly large in some Orthopteroid insects, and serves as a pivotal structure for the antenna in these insects. The scape, *sc* of Fig. 11, is the large, broad, rather flat, basal segment of the antenna. The next segment or pedicel *pd* and the segment beyond it, or the postpedicel *ppd,* are subequal in size. The postpedicel *ppd* is usually regarded as the first segment of the flagellum, or that portion of the antenna distal to the pedicel *pd.* In the flagellum we may distinguish two main types of segments, the brachymeres or short segments, and the dolichomeres, or long segments. The brachymeres in turn consist of long brachymeres labeled *lb* in Fig. 11, and short brachymeres labeled *sb,* while the dolichomeres consist of broad dolichomeres *bd,* intermediate dolichomeres *id* and slender dolichomeres *sd* (at the tip of the antenna). The scape of the antenna is somewhat flattened to enable the antenna to lie close to the head, when the antennæ are laid back along the head to get them out of the way during the digging operations of the insect, and the compound eyes, *e* of Fig. 5, project slightly in their dorso-mesal region so that the antennæ can be laid back above the eyes, and may be protected to some extent by the projecting eyes (the antennæ apparently have but little freedom of movement basally, since the scape seems to move backward and forward, but has not much lateral movement, so that the eyes doubtless prevent straining the antennæ basally by furnishing some support for the scape when the latter is pressed backward during the digging operations of the insect).

The compound eyes, *e* of Fig. 5, are situated rather far down the sides of the head, and they are not very large. Our eastern "cave cricket," *Ceuthophilus,* exhibits a similar tendency toward the reduction of the compound eyes, and even *Grylloblatta,* which is very like the ancestors of all of these forms, has very small eyes (see Crampton, 1926). The hiding habits of these insects doubtless put a premium upon relatively small eyes and correspondingly well developed antennæ, and in insects with hiding habits we frequently find the development of sensitive antennæ correlated with a reduction of the eyes, enabling those forms which exhibit this tendency to establish themselves in caves and similar situations more readily than other types of insects. The reduction of the eyes is thus due not so much to "disuse," as it is to the fact that antennal development (useful in the dark) is correlated with eye reduction. The ocelli are vestigial or lacking (what appear to be very faint traces of them can be barely made out) and in this respect *Stenopelmatus* likewise resembles *Ceuthophilus* and *Grylloblatta.*

When the head is removed and is viewed from the rear, as in Figs. 13 and 6, one may readily observe a large posterior opening called the occipital foramen, or foramen magnum, *ocf,* through which the gullet, nerve cord, etc., pass backward from the head capsule into the neck and prothoracic region. On each side of the foramen is a lateral sclerite *po,* or paroccipiut, which is considered by Riley (1904) to be the pleural region of the labial segment. It is separated by a rather pronounced groove, the paroccipital groove, from the rest of the head capsule; and at the ventral end of the groove is located the gular pit, *gp* of Figs. 6 and 12, which is formed by an invagination or inpushing of the chitin to form a posterior arm of the tentorium presently to be described. Ventral to the gular pit, *gp* of Fig. 12, is a paragular process, *pap,* over which a basal projection of the maxillary cardo rides (i. e., the projection labeled *d* in Figs. 13, 10, etc.). The sclerite *po* bears an occipital condyle, *occ* of Figs. 13 and 6, for articulation with the anterior end of the lateral cervical or neck plate. The endocciput, *eo* of Fig. 13, is an internal ridge formed by an infolding of the integument between the sclerite *po* and the cranium proper. A dorsal paroccipital tendon *pat* is attached near its dorsal portion, and is a tendon of muscles extending to the thoracic region. The sclerite, *eoc* of Fig. 13, is a demarked median dorsal region called the euocciput or surocciput, and near its anterior margin (internally) is attached a median dorsal tendon *eot* of a muscle extending to the thoracic region. The sclerites *po* and *eoc* are parts of the occiput, or occipital region of the head.

Lateral to the parocciput, *po* of Figs. 13, 6, 12, etc., is the postgena *pge* which is separated from the gena *ge* by the postgenal suture *pgs.* Ventrally, there is demarked in the postgenal region a marginal area, the parastome or hypostoma *pst,* extending along the ventral edge of the posterior region of the head capsule. This marginal area *pst* bordering the mouth region posterolaterally is rather illy defined in *Stenopelmatus,* but in certain beetles it forms an important sclerite. In this general region are the projections *pap* of Fig. 12, over which the process *d* of the cardo rides (Fig. 10), and the projection *pp* (Figs. 13 and 3), which bears a cup-like acetabulum *pga* (Fig. 3) for the posterior condyle of the mandible *h.*

The mandible has three principal surfaces best noted when the mandible is removed and viewed basally (i. e., looking down into its hollow interior), as in Fig. 2. The outer or lateral surface bears a lateral prominence *ep* to which is attached the extensor tendon *et* of the muscle opening the mandible, and the outer surface (in section) forms the base of a triangle at the apex of which is the mesally located structure *gn* of Fig. 2, bearing the flexor tendon *ft* of the muscles closing the mandible. The ginglymus *g* (Fig. 2) is an anterior projection presently to be described, and the condyle *h* is a posterior projection which will be discussed later. From *g* to *gn* in Fig. 2 is the anterior surface, and from *h* to *gn* is the posterior surface, and *gn* is located at the base of the median ridge of the mandible, best shown in Fig. 4. The endognath *eg* of Fig. 2 is a basal internal shelf projecting inward and extending around the basal portion of the mandible.

In Fig. 4 is shown a posterior view of the insect's left (sinistral) mandible; and seen in this view, the mandible appears to taper distally (ventrally) to form the gnathapex *ga.* Dorsal to this region, along the median ridge of the mandible, is the grinding area or mola *m* of Fig. 4; and dorsal to the mola is the brush or brustia *br.* At the base of the median ridge of the mandible is the gnathite *gn,* which bears the flexor (closing) tendon *ft* (compare *gn* and *ft* of Fig. 2). On the opposite or outer surface of the mandible is the projection *ep* bearing the extensor (opening) tendon *et,* behind which is the condyle *h* (compare also *ep* and *h* of Fig. 2). On the posterior surface of the mandible is the gnathal impress *gs* of Fig. 4, or depression marking the position of an internal projection for muscle attachment, etc.

If the basal region of the mandible shown in Fig. 2 is turned back up in the normal position, as shown in Fig. 3, it will be seen that the posterior condyle *h* fits into an acetabulum *pga* borne on the process labeled *pp* in Figs. 3, 1, and 13; and the anterior ginglymus *g* of Figs. 2, 3, etc., is received into a niche or incision in the lateral margin of the postclypeus *pc* as is shown in Figs. 3 and 1, where the incision is labeled *ct*. The ginglymus *g* of Figs. 2 and 3 is likewise grooved, and fits over a ridge (clypeothecal ridge) near the incision *ct* which receives the projecting ginglymus, *g*. The epignath, or lateral prominence *ep* of the mandible (see Fig. 2), dips beneath the basimandibular sclerite *bm* of Fig. 1, when the mandible is opened (see also Fig. 5) and its tendon *et* extends dorsad on the mesal side of the anterior arm of the tentorium labeled *pt* in Fig. 3. If a line is drawn between the points labeled *g* and *h* in Fig. 2, it will be seen that the point of attachment of the extensor tendon *et* borne on the prominence *ep*, lies outside of, or lateral to this line between *g* and *h* (compare Fig. 4), so that when the mandible rocks or pivots on the points *g* and *h*, a pull exerted at the point *ep* of Fig. 2 would open the mandible; and since the muscle opening the mandible need not be very powerful, the tendon attached at this point is a slender one. When the mandible pivots on the points *g* and *h* of Fig. 2, and a pull is exerted at the point *gn*, the mandible would be closed; and since the closing muscles must be very powerful for chewing food, etc., the flexor tendon *ft* exerting a pull at *gn* is a hugely developed tendon (see also Fig. 4). As is shown in Fig. 4, the flexor tendon *ft* is not attached directly to the mandible itself, but is borne on a sclerite-like structure, the gnathite *gn*, which is itself attached to the mandible by a membrane.

In describing the parts of the maxilla, I have employed the terminology used in a paper in which the maxillæ were compared throughout all of the orders of insects (Crampton, 1923); and I would again call attention to the homologies pointed out in this paper, since the facts brought out in the article in question are completely ignored by recent entomologists who misinterpret the basal region of the stipes for the entire stipes in the Coleoptera, and misidentify the parastipes of Orthopteroid insects with the so-called subgalea described by coleopterists who mistook the inflexed edges of underlying sclerites for sutures in the plates situated above them in balsam mounts of maxillæ, and applied the designation subgalea to a supposed area situated below the galea (or in reality dorsal to the galea) wholly different from the parastipes here described. Since there is not space here for a full discussion of the parts in different insects, the reader is referred to the above-mentioned article for a comparison of the parts in different insects, and the reasons for the views concerning the homologies here accepted.

In Fig. 13 is shown a posterior view of the insect's right or dextral maxilla. The basimaxillary membrane, labeled *b,* connects the maxilla with the labium (and with the hypopharyngeal region). The basal segment or cardo is divided by the cardinal suture, *cds* of Figs. 10 and 13, into a basicardo *bc* and disticardo *dc.* An internal ridge or endocardo, *ec* of Fig. 8, corresponding to the external cardinal suture, extends along the inner face of the cardo and serves to strengthen the cardo and likewise offers a point of attachment to certain of the muscles inserted upon the inner surface of the cardo. The cardoprocess, *cp* of Figs. 8 and 10, is an inner process to which the cardo tendon *ctn* is attached. This tendon enables the extensor or opening muscles of the maxilla to exert a pull at the point *cp,* while the region under the process, labeled *d* in Fig. 10, serves as a fulcrum or pivotal point in opening the maxilla. The process, labeled *d* in Figs. 10 and 8, rides over the ridge *pap* of Fig 12, while the process *cp* lies on the inner side of the ridge *pap,* so that the process *cp* of Fig. 10 is not visible from the exterior, while the process *d* of Fig. 10 is visible from the exterior, as is shown in Fig. 13.

The endostipes *est* of Fig. 8 is an internal ridge which serves to strengthen the walls of the stipes, and furnishes attachment for certain of the muscles which serve to close the maxilla, or to draw it toward the labium. The endostipes *est* of Fig. 8 corresponds to the external parastipital suture which demarks the parastipes *ps* of Fig. 13. The parastipes *ps* is not homologous with the so-called subgalea, although MacGillivray and others have mistakenly supposed that these two sclerites are the same. In many Coleoptera, Dermaptera, certain Gryllotalpids, etc., the stipes *s* of Fig. 13 is divided into a basal region and a distal region *ds,* but in *Stenopelmatus* the basal region is not demarked, although the distal region *ds* is faintly demarked by a somewhat indistinct suture. The region *ds* is external to the point of attachment of the laciniatendon *lt* of Fig. 8, or the internal tendon attached to the base of the lacinia *la*. When this tendon exerts a pull upon the lacinia the lacinia apparently pivots upon the end of the endostipital ridge *est* of Fig. 8, although the lacinia does not seem to be very mobile. An anterior view of the lacinia is shown in Fig. 9, in which the tooth-like processes of the lacinia are labeled *ld,* the lacinia-mobilis-like process is labeled *lii,* and the lacinial fringe is labeled *gf*. The basigalea *bg* and distigalea *dg,* or basal and distal segments of the galea, are more clearly demarked in the anterior region shown in Fig. 9 than in the posterior region shown in Fig. 13. The palpifer *pf* of Fig. 13 is fairly clearly demarked, and the maxillary palpus *mp* which it bears is composed of the five segments typical of lower insects. The fifth segment bears a sensory area which is stippled in Fig. 13.

The labium is shown in Fig. 13. The glossæ *gl* are fairly well developed, and the glossæ with the paraglossæ *pgl* are borne on the glossigers *gg,* which in turn are borne at the distal ends of the sclerites *li,* which represent the labial stipites, while the glossæ and paraglossæ represent the laciniæ and galæ of the labium. Basolaterad of the sclerites *li* are the palpigers *pg,* which correspond to the maxillary palpifers and bear the palpi *lp* which are reduced to three segments in the labium of Orthopteroid insects. The sclerites representing the maxillary cardines are vestigial, although some investigators maintain that the mentum *mn* represents the united cardines, while others think that the cardines are represented by the submental region. The mentum *mn* is distinct and quite well developed in *Stenopelmatus,* and is somewhat suggestive of the mentum of a cricket. The submentum *sm* and gula *gu,* though differing in color, are merely regions of a single plate in most Orthopteroid insects, and the gula *gu* is not united with the head capsule in *Stenopelmatus,* although the gular pits *gp* of Fig. 12 are situated near the gula *gu*. The gular pits *gp* are the mouths of the invaginations forming the posterior arms of the tentorium presently to be described. The postgular plate *pgu* of Fig. 13 is a ventral cervical plate, which will be described in discussing the neck region of *Stenopelmatus*.

In Fig. 6 the labium has been removed and the parts of the tentorium are shown as though cleared of the muscles and other concealing structures, which were removed by boiling in 10 per cent caustic potash. The gular pits, which were mentioned above, are labeled *gp* in Fig. 6. The invaginations from the gular pits form the posterior arms of the tentorium, which unite to form the eutentorium or body of the tentorium, labeled *eu* in Fig. 6, and they also form the posterior arch, labeled *p* in Fig. 6. Behind the arch *p* are the two posterior processes, labeled *pop,* which bear the posttentorial tendons, labeled *pot.* A deep emargination or incision, labeled *nf* in Fig. 6, forms the neural incision, which apparently corresponds to the neuroforamen of the roach, etc. (see description by Crampton, 1925). The anterior arms of the tentorium, labeled *pt* in Fig. 6, extend backward from the frontal pits, *fp* of Fig. 5, and give off the dorsal arms of the tentorium, labeled *st* in Fig. 6. At the distal ends of the structures, labeled *st,* are borne the delicate structures, labeled *dt* in Fig. 6, which are apparently distal portions of the dorsal arms of the tentorium.

The hypopharynx *hp* is shown in Fig. 15. The hypopharynx of *Stenopelmatus,* like that of the roach figured by Crampton (1925), is composed of a distal region *dl,* or distilingua, and a basal region *bl,* or basilingua. The salivary glands, which are not shown in Fig. 15, open in the ventrobasal region of the basilingua, *bl.* The slender sclerite, labeled *ll* in Fig. 15, apparently corresponds to the sclerite called the lingualora in the roach, and the sclerite, labeled *pl,* corresponds to that called the linguatendon in the roach. Since the sclerite *pl* is not exactly a tendon, it is preferable to refer to it as the postlingua in *Stenopelmatus.* The dorsal portion of the base of the hypopharynx, labeled *sl* in Fig. 15, lies below the posterior epipharyngeal region, labeled *poe* in Fig. 15.

The regions labeled *poe* and *pre* in Fig. 15 are the posterior and anterior regions of the epipharynx or portion of the roof of the mouth. The posterior region *poe* is situated in the clypeal area, while the anterior region *pre* is situated in the labral area. In Fig. 7 these areas of the epipharynx are shown in an inner or buccal (pharyngeal) view of the labrum and clypeal region. The tormæ *to* of Fig. 7 demark the labrum from the clypeus in this view. A narrow transverse sclerite *it* extends between the tormæ *to* and serves to demark the anterior epipharyngeal region *pre* from the posterior epipharyngeal region *poe*.

In discussing the relation of the maxilla to the underlip, it should have been mentioned that the distal margin of the maxillary membrane *b* merges into the distal margin of the submentum *sm*, as shown in Fig. 13. The attachment of the basimaxillary membrane *b* may therefore be taken as a landmark for demarking the distal limits of the submentum in *Stenopelmatus* and certain other insects. In higher insects, however, this criterion for determining the distal limits of the submental region does not hold good, so that this feature is not of universal application (see discussion by Crampton, 1928).

The external anatomy of the thoracic and abdominal regions will be discussed in another paper, since it is possible to devote more space to the description of the parts, and more plates to illustrating the anatomical details of the various regions, if these are treated in a series of papers, instead of trying to include the descriptions of all of the main external features of *Stenopelmatus* in a single paper.

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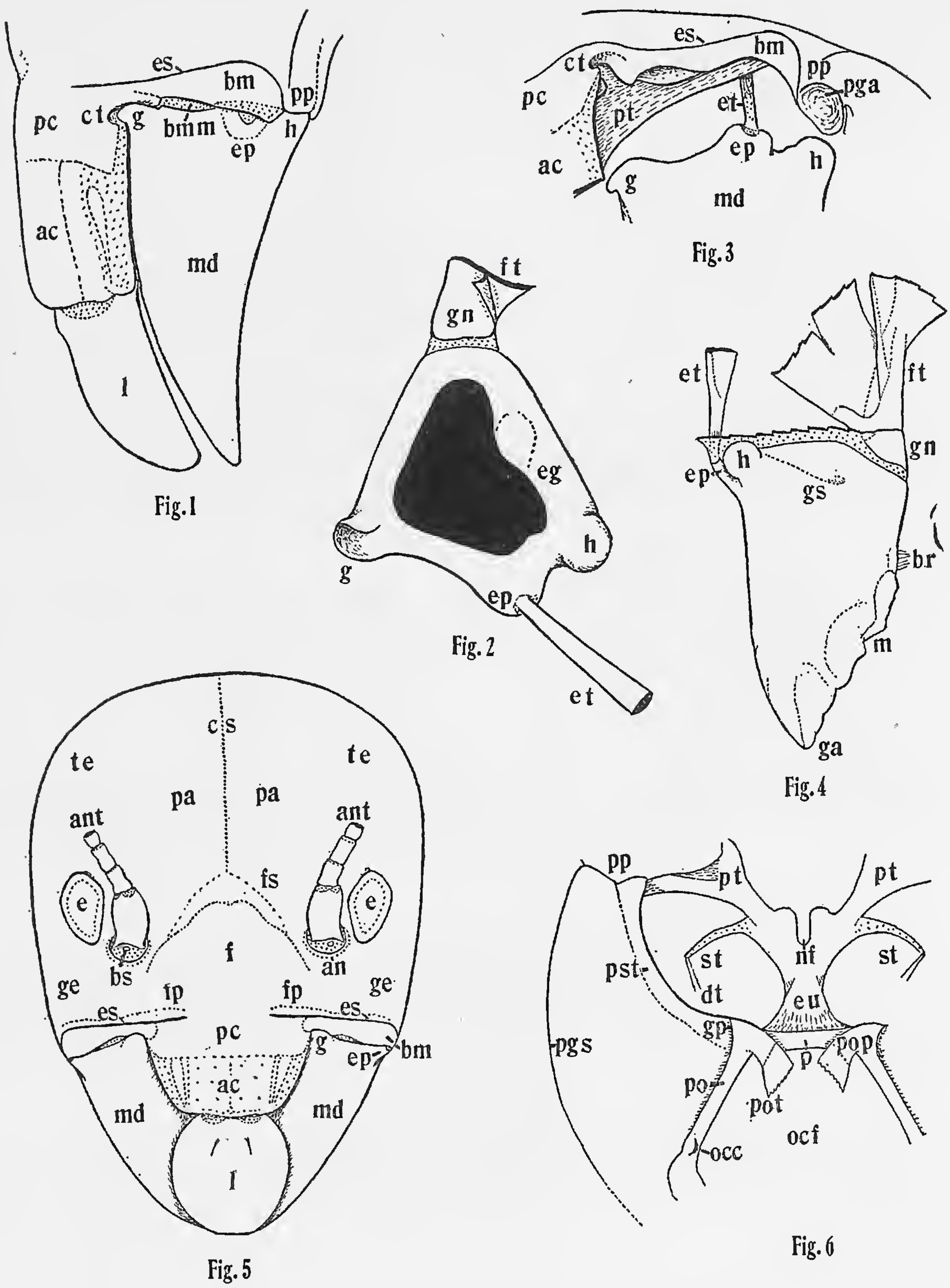
## Abbreviations

ac. Anteclypeus
af. Antennifer
an. Antennale
ant. Antenna
b. Basimaxillary membrane
bc. Basicardo
bd. Broad dolichomeres of antenna
bg. Basigalea
bgl. Basiglossa
bl. Basilingua
bm. Basimandibulare
bmm. Basimandibular membrane
br. Brustia
bs. Basiscape
c. Clypeus.
cds. Cardosuture
cp. Cardoprocess
cs. Coronal suture
ct. Clypeotheca
ctn. Cardotendon
d. Epicardo
dc. Disticardo
dg. Distigalea
dl. Distilingua
ds. Dististipes
dt. Distitentorium
e. Compound eye
ec. Endocardo
eg. Endognath
eo. Endocciput
eoc. Euocciput or surocciput
eot. Euoccipital tendon
ep. Epignath or extensor prominence
es. Epistomal suture
esp. Endostipital process
est. Endostipes
et. Extensor tendon
eu. Eutentorium or body of tentorium
f. Frons or front
fp. Frontal pits or clefts
fs. Frontal sutures
ft. Flexor tendon
g. Ginglymus
ga. Gnathapex
ge. Gena
gf. Laciniafimbrium
gg. Glossiger (basiglossa)
gl. Glossa
gn. Gnathite
gp. Gular pits.
gs. Gnathal suture or impress
gu. Gula
h. Gnathocondyle or hypocondyle

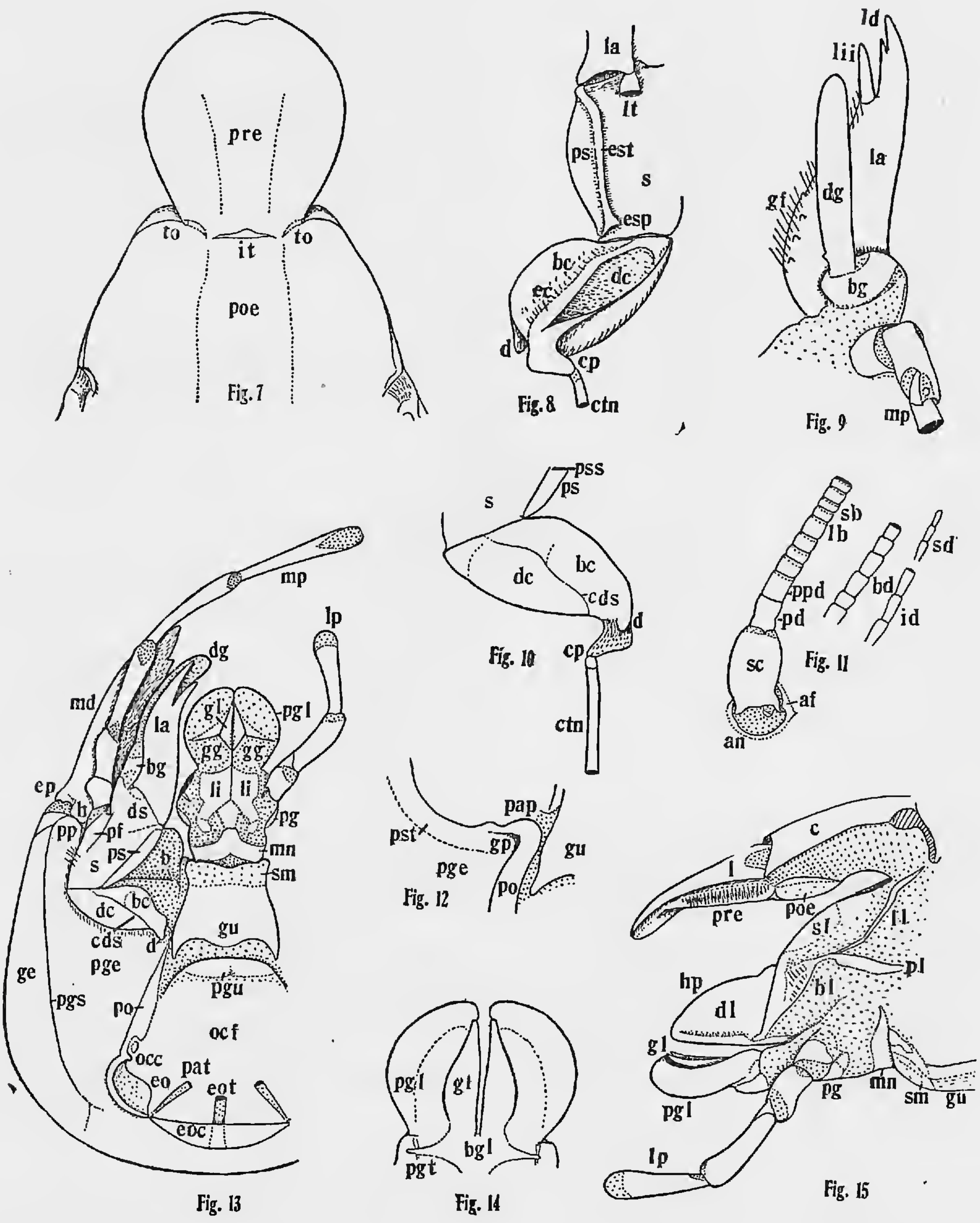
hp. Hypopharynx
id. Intermediate dolichomeres of antenna
it. Intertorma
l. Labrum
la. Lacinia
lb. Long brachymeres of antenna
ld. Laciniadentes
li. Labiites or labial stipites
lii. Lacinula
ll. Lingualora
lp. Labial palpus
lt. Laciniatendon
m. Mola
md. Mandible
mn. Mentum
mp. Maxillary palpus
nf. Neuroforamen or neural incision
occ. Occipital condyles
ocf. Occipital foramen or foramen magnum
p. Tentorial arch or trabecula
pa. Parietalia
pap. Paragular or paroccipital process
pat. Paroccipital tendons
pc. Postclypeus or epistoma
pd. Pedicel
pf. Palpifer
pg. Palpiger
pga. Postgenal acetabulum
pge. Postgenæ
pgl. Paraglossæ
pgs. Postgenal suture
pgt. Paraglossal tendon
pgu. Postgulare
pl. Postlingua or "linguatendon"
po. Parocciput
poe. Postepipharynx
pop. Posttentorial process
pot. Posttentorial tendon
pp. Postgenal process
ppd. Postpedicel
pre. Preepipharynx
ps. Parastipes
pss. Parastipital suture
pst. Parastomium
pt. Pretentorium
s. Stipes.
sb. Short brachymeres of antenna
sc. Scape
sd. Slender dolichomeres of antenna
sl. Dorsolingua (surlingua)
st. Supratentorium
te. Tempora
to. Tormæ

## Explanation of Plates

Fig. 1—Lateral view of sinistral mandible, clypeus and labrum; Fig. 2—Dorsal view of base of sinistral mandible; Fig. 3—Lateral view of base of mandible and neighboring parts; Fig. 4—Posterior view of sinistral mandible; Fig. 5—Frontal view of head; Fig. 6—Posterior view of tentorium and neighboring parts; Fig. 7—Inner or buccal view of labrum and clypeus; Fig. 8—Inner surface of cardo and stipes; Fig. 9—Anterior view of lacinia and galea; Fig. 10—Basal portion of dextral maxilla (posterior view); Fig. 11—Parts of antenna; Fig. 12—Posterior view of region at base of gular plate; Fig. 13—Posterior view of back of head; Fig. 14—Anterior view of glossæ and paraglossæ; Fig 15—Lateral view of hypopharynx and upper and lower lip, with most of the head capsule removed.




Crampton. Head structures of Stenopelmatus. For explanation see page 108.




Crampton. Head structures of Stenopelmatus. For explanation see page 108.